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The northernmost discovery of a Miocene proboscidean bone in Europe

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ABSTRACT

We discuss a proboscidean bone fragment discovered in southern Finland, including the morphological analysis of the bone, as well as pollen and diatom analyses from sediment contained in the marrow cavity. Preliminary analysis of the bone suggested petrification and thus an apparently old age, while the microfossil assemblages include numerous unequivocally pre-Quaternary pollen, spore, and diatom types. A Miocene age for the bone is determined based on the presence of the diatom genus *Alveolophora*, indicating a minimum age of 5 Ma, and based on the earliest appearance of proboscideans outside Africa, setting a maximum age of 19 Ma. Based on morphology, the bone is determined as a partial humerus of the left foreleg of a large proboscidean. The bone is tentatively assigned to cf. *Deinotherium* sp., which is consistent with the diatom-based minimum age. The pollen assemblage is rich in spores of shoreline pteridophytes, while the diatom assemblage is also consistent with a shoreline freshwater environment, suggesting that the bone was deposited post-mortem near the shore of a lake or a stream. Miocene sediments do not currently exist in southern Finland or in the near vicinity. This implies that the bone has been transported over a considerable distance. Due to the discovery of the bone in early-Holocene Baltic Sea clay, the final transport phase and deposition must have taken place via iceberg rafting. This was likely preceded by one or more phases of glacial and/or glacio-fluvial transport. While we are unable to conclusive ascertain the region of origin, the alkaline composition of the contained sediment and diatoms point towards the Russian Plain region in the east. This specimen represents the oldest mammalian bone discovered in Finland and the northernmost discovery of a Miocene proboscidean bone in Europe.

Keywords: Finland, *Deinotherium*, Neogene, pollen, diatoms, environmental reconstruction

INTRODUCTION

Discovery of the bone

In about 1960, a 25-cm-long bone fragment was found during autumn gardening at a lake-shore "summer house" situated in the municipality of Suomusjärvi, southern Finland (Fig. 1a–b). The finder, young biology student Marja Sorsa, discovered the bone fragment in sandy clay at a depth of about 50–60 cm. The piece, first thought to be a remnant of a ploughing ox or a piece of a mammoth, was stored in a cardboard box in a garden shelter. The bone was later removed from its original finding site into a city garage storage and forgotten until finally in 2006, the finder (M.S.) presented the bone to professor Mikael Fortelius at the meeting of the Finnish Academy of Science and Letters. The bone was identified as a partial humerus of the left foreleg of a proboscidean. Due to its big size and structure, the original hypothesis was that the bone belongs to a proboscidean of Quaternary age, as all fossil mammal specimens previously discovered in Finland have been of late Quaternary or Holocene age, including the ten finds of woolly mammoth (e.g. Ukkonen et al., 2011) the oldest of which is dated to ca. 120 ka (Ukkonen et al., 2010). However, the Suomusjärvi bone raised special interest as it was partly eroded and heavy, possibly indicating a petrification and thus a greater age. As the then available information was too sparse for inferring the age of the bone, we performed sedimentological and microfossil analyses (pollen, diatoms) in order to estimate the age and the depositional environment of the bone. In addition, the morphology and structure of the bone were thoroughly investigated.

[Figure 1]

Geological setting

Finland is situated at the centre of the area covered by the Scandinavian Ice Sheet during the Late Pleistocene, and thus in the vicinity of large periglacial centres of terrestrial mammals in Europe and Siberia (Ukkonen, 2001). The Finnish geological setting is mainly composed of Precambrian bedrock (with some small bits of Palaeozoic), stripped clean of younger layers by repeated glacial erosion during the Pleistocene, with the crystalline Precambrian bedrock typically only overlain by glacial deposits of the last glaciation. As the repeated glaciations have generated a landscape consisting of bedrock that is up to 3.2 Ga old and a sediment layer less than 20 ka old, practically no fossil bearing deposits have survived (Ukkonen, 2001). For example, deposits of the Neogene or the Palaeogene do not exist in southern Finland. In contrast, isolated remains of sediments representing these periods have been preserved in northern Finland, where Pleistocene glacial erosion has been weaker due to the location closer to the Fennoscandian ice divide. These deposits include the Palaeogene marine clay at Akanvaara, as well as a Neogene freshwater diatomite in Naruskajärvi (Hirvas and Tynni, 1976; Tynni, 1982; Rasmussen et al., 2008).

The site of bone discovery is situated in the west of Lake Enäjärvi, in the municipality of Suomusjärvi, in southern Finland (60°17′47″N 23°38′28″E) (Fig. 1a). Today the site is located 60 m above the present sea level. The bone was found in clay sediment covered by a thin agricultural soil, at a depth of about 50 cm. The depth and character of the clay layer was confirmed in a later excavation in 2006 (Fig. 1c). The area was released from the late Weichselian ice sheet at the onset of the Holocene around 11,500 years ago (Saarnisto and Saarinen, 2001), and the site of discovery is located between the Salpausselkä II and III ice-marginal formations. In the Baltic Sea history, this timing corresponds with the Yoldia Sea stage, which started when the Baltic Ice Lake was drained to ocean level through channels in central Sweden and water level dropped around 25 m in the Baltic basin ca. 11,700 years ago (e.g. Björck, 1995). During the Yoldia Sea stage, clayish sediments and ice-rafted material from icebergs accumulated at the site within the water depth of around 60 m at this time.

Outline of this study

Examination of the bone revealed hard-packed brownish silty sediment preserved in the bone marrow cavity (Fig. 1b,d). As microfossils such as pollen and diatoms often contain useful chronological and environmental indicators, the preservation of the sediment thus presents an opportunity to provide further constrains on the history of the bone, both in terms of its age and its geographic origin, as well as the systematic determination of the animal.

Here we present the results of a multidisciplinary investigation into the origin of the Suomusjärvi bone, including (A) the analysis of the bone fragment itself, (B) pollen and diatom analyses for the sediment contained within the bone, and (C) consideration of the geological context and processes in the setting in which the bone was found. In assessing the results we especially focus on the following four questions:

1. Is it possible to provide a species or genus level identification for the animal based on bone morphology and size?
2. Is it possible to narrow down the age of the bone based on the species identification together with the microfossil assemblages?
3. Is it possible to reconstruct the living environment of the animal based on the microfossil assemblages?
4. If yes, does the environmental reconstruction help confirm the geographical origin of the bone?

METHODS

Analysis of the bone

The specimen from Suomusjärvi is confirmed to be a fragment of a left humerus diaphysis of a proboscidean. We describe the specimen systematically and compare it with other published proboscidean humeri from the Neogene of Europe. The preservation of the specimen is discussed. Linear osteometric measurements were taken on 1 mm precision with a digital caliper, and minimum circumference was measured with a flexible measuring tape. The measurements were taken following Göhlich (1998) and Huttunen and Göhlich (2002). Minimum depth of the diaphysis was measured from the location of minimum width in the bone. The specimen was weighed at 1 g precision using a digital scale.

Sedimentological analysis

The composition of the fine fraction sediment preserved in the bone was carried out by the Field Emission Scanning Electron Microscope (SEM) method in the Research Laboratory of the Geological Survey of Finland.

Pollen analysis

A pollen sample was prepared from ca. 1 cm^3 of sediment using KOH and HF treatments (Moore et al., 1991). The entire residue was mounted in silicone oil on six slides and analysed using a light microscope. The pollen were identified using literature on modern European (Moore et al., 1991; Reille, 1992) and Asian (Wang et al., 1997) pollen types, supplemented with literature on European Neogene palynology (Shatilova and Stuchlik, 1996; Grímsson and Zetter, 2011; Grímsson et al., 2011).

Diatom analysis

The diatom sample of ca. 1 cm^3 was prepared using standard methods (Battarbee, 1986). A Nikon microscope with 1000x magnification was used for the identification of diatoms. One hundred valves were counted in the sample. The taxonomy is based on the following sources: Mölder and Tynni (1967–1973), Tynni (1975–1980), Ross et al. (1979), Krammer and Lange-Bertalot (1986–1991), and Usoltseva et al. (2013).

RESULTS

Bone

Systematic description and comparison

Order Proboscidea Illiger, 1811

cf. *Deinotherium* Kaup, 1829 sp.

Material – humerus (sin.), partial diaphysis

Description

The specimen from Suomusjärvi is a fragment of the diaphysis (shaft) of a left humerus, belonging to a large-sized proboscidean (Fig. 2). It is fully re-mineralised and heavy for its size, with a mass of 3045 g. The specimen is approximately from the middle of the shaft, preserving the narrowest part of the bone. Measurements of the specimen are shown in Table 1. Despite the fragmentary nature of the specimen, the middle part of the shaft is relatively well preserved in the caudal and lateral surfaces. The cranial surface is more eroded, especially in the proximal part of the specimen, but less so in the distal part which represents the narrowest part of the diaphysis. In the distal end of the specimen, the proximal-most edge of the crista

189 supracondylaris lateralis is partly preserved. The proximal part of the specimen shows a slightly
190 cracked and eroded proximal edge of crista humeri. The crista humeri overall is not prominent
191 and the sulcus musculus brachialis is shallow, making the cross-section of the narrowest part of
192 the shaft rounded rather than triangular in shape. This is likely to approximately represent the
193 original morphology of the bone, because despite the slight fragmenting and erosion of the
194 surface of the specimen, there does not appear to be major distortion to the middle of the shaft.
195 Because the epiphyses are not preserved, it is impossible to estimate how fused they were,
196 making it impossible to estimate the age or growth stage of the individual animal.
197
198 [Figure 2]
199 [Table 1]
200
201 *Comparison and discussion*
202
203 The lack of a prominent crista humeri and the subsequently shallow sulcus musculus brachialis,
204 as well as the relatively rounded cross-section of the Suomusjärvi proboscidean humerus
205 diaphysis, are features characteristic for the genus *Deinotherium* Kaup, 1829 (see Huttunen,
206 2004; Kovachev and Nikolov, 2006) (Figs 2–3). However, the fragmentary nature of the
207 specimen raises some concern about the preservation of these features. In contrast to the
208 Suomusjärvi specimen, gomphotheres (Gomphotheriidae) and mammutids (Mammutidae)
209 typically exhibit strong crista humeri which sometimes result in an almost triangular rather than
210 rounded cross-section of the middle of the humerus shaft (e.g. Göhlich, 2010; Tsoukala and
211 Mol, 2014). Also the earlier, on average smaller-sized deinothere genus *Prodeinotherium* differs
212 from *Deinotherium* in having a strong crista humeri and deep sulcus musculus brachialis
213 (Huttunen, 2004). The reduced crista humeri of *Deinotherium* compared to other proboscidean
214 taxa is visually shown in Fig. 4. In elephantimorphan proboscideans (Mammutidae,
215 Gomphotheriidae and Elephantidae, sensu Shoshani and Tassy, 2005) the middle part of the

humerus shaft tends to be relatively deep in relation to its width, although there is considerable variation, whereas in deinotheres the mid-shaft is craniocaudally somewhat flattened. This is demonstrated by significantly higher average width/depth ratios in deinothere humeri than in the humeri of mammutids, gomphotheres and elephants (Fig. 5). In this respect also, the Suomusjärvi specimen is closer to the average of deinotheres than to the mammutids, gomphotheres and elephants (Fig. 5), although this characteristic does not definitely exclude the other taxa. We tentatively assign this specimen to cf. *Deinotherium* sp.

[Figure 3]

[Figure 4]

[Figure 5]

Measurements of the Suomusjärvi specimen fit with those reported for some specimens of *Deinotherium*, but are relatively small for that genus (Table 1). In particular, the Suomusjärvi specimen is close in size to the *Deinotherium giganteum* specimen from Munich described by Stromer (1938). Another example of a comparable medium-sized *Deinotherium* is the partial skeleton from the late Middle Miocene locality of Gratkorn, Austria, identified as *Deinotherium levius* or early *D. giganteum*, although this skeleton lacks humeri almost entirely (Aiglstorfer et al., 2014). Erosion of the Suomusjärvi specimen could have had some (but probably not major) effect on its measurements. It is also worth noting that because the epiphyses of the bone are lacking, we cannot estimate the age or growth stage of the individual, which makes it impossible to estimate whether it was a juvenile or a fully grown animal. This is particularly relevant in the case of proboscideans which continue to grow throughout their life. Other reported specimens of European *Deinotherium*, of presumably younger geological age, are notably larger in size and have variably been assigned to the species *D. giganteum* (e.g. Bachmayer and Zapfe, 1976; Huttunen, 2002; Christiansen, 2004), *D. gigantissimum* (Stefanescu, 1894; Markov, 2008), *D. thraceiensis* (Kovachev and Nikolov, 2006), or *D.*

243 *proavum* (e.g. Pickford and Pourabrishami, 2013).

244

245 **Sediment properties**

246

247 The mineral composition of the clayish fine fraction preserved in the bone differs from that of
248 clay sediments in Finland, including the finding site. The sediment in the marrow cavity appears
249 to originate from more alkaline bedrock compared to the Fennoscandian Shield region in which
250 the bone was found. Such sediments are common further east, e.g. in today's Russia.

251

252 **Pollen content**

253

254 The pollen density in the sediment was extremely low, with only 147 palynomorphs counted
255 from the entire residue remaining from ca. 1 cm^3 of sediment. The condition of the
256 palynomorphs was often (but not exclusively) poor, and only 98 palynomorphs could be
257 identified, with 49 left unidentified as degraded and/or broken (37 grains), obscured (9) or
258 unidentified (3). The identified palynomorphs (Table 2) are a combination of various Pre-
259 Quaternary types, exotic to modern Europe, and types closely resembling modern and Late-
260 Quaternary North European pollen.

261

262 [Table 2]

263

264 The most commonly occurring palynomorph, at 26.5 % abundance, is a large, tuberculate type
265 of trilete spore (Fig. 6a–c). Well-preserved specimens of this type match excellently the
266 description of the fossil species *Pteridacidites variabilis* Stuchlik & Shatilova, 1996, with ca.
267 50–55 μm equatorial diameter, sides from polar view either straight or slightly convex but never
268 concave, tuberculate exine with the tubercles on the proximal face concentrated around the
269 laesura to form a ridge-like shape (Fig. 6a) while tubercles on the distal side coalesce to form

sinuous shapes (Fig. 6c) (but never a reticulum as seen in some other *Pteridacidites* fossil species; Shatilova and Stuchlik, 1996), and the width of the equatorial collar 4–7 μm with the collar sometimes but not always narrowing at the angles (Shatilova and Stuchlik, 1996). Little variability is seen in size, shape or ornamentation between individual spores, and the examples shown in Fig. 6a–c are representative. Shatilova and Stuchlik (1996) regard *Pteridacidites variabilis* as the probable closest ancestor of the modern *Pteris cretica* L. (Cretan brake fern). The spores here designated as *Pteridacidites variabilis* also very closely resemble those of modern *Pteris cretica* (Reille, 1992; Shatilova and Stuchlik, 1996).

[Fig. 6]

The second-most commonly occurring type, at 15.3 % abundance, is a small (equatorial diameter ca. 20–22 μm), echinate trilete spore (Fig. 6d). These are comparable with the spores of modern *Selaginella* species (but not the much larger spores of *S. selaginoides* type which occur in late-Quaternary sediments of northern Europe). Consequently, they are here placed within *Echinatisporis*, a fossil genus used for *Selaginella*-type spores (e.g. Grímsson et al., 2011).

Monolete, bean-shaped spores resembling the modern *Dryopteris*-type occur at 12.2 %. In addition, the sample includes smaller numbers of other, large trilete spores of types not encountered in late-Quaternary sediments of northern Europe (an example in Fig. 6e).

A final clearly pre-Quaternary feature is the occurrence of pollen grains of Cupressaceae (but representing types other than *Juniperus* which also occurs in the North-European Quaternary). These are small (diameter 22–28 μm) and round inaperturate grains, either fractured (Fig. 6f) or collapsed (Fig. 6g) in the thin-walled germination area. Numerous Cupressaceae tree species were elements in Palaeogene and Neogene forests of Europe, up to the Pliocene (Grímsson and

297 Zetter, 2011). It is not possible to identify these specimens to genus level, as critical diagnostic
298 features such as the papilla are not preserved or visible (Grímsson and Zetter, 2011).
299
300 The remaining palynomorphs (Table 2) represent types which occur in both Neogene and
301 Quaternary sediments of Europe (*Pinus*, Poaceae, *Betula*, *Artemisia*, Chenopodiaceae, *Alnus*,
302 *Equisetum*, and *Juniperus*).
303
304 **Diatom content**
305
306 The investigated sediment sample was abundant in diatoms. They were very well preserved and
307 in good condition, and the diatom assemblage was uniform suggesting a consistent
308 sedimentation environment. This indicates that the analyzed sediment sample is not redeposited.
309 The results of the diatom analysis are presented in Table 3 and micrographs of the most
310 commonly occurring types in Fig. 7. The diatom assemblage was unilateral, i.e. a few diatom
311 species dominate the flora. The most common diatom species were the (mero)planktonic
312 *Alveolophora* sp. and *Aulacoseira granulata* (Ehrenberg) Simonsen (1979), covering about 90
313 % of the total diatom sum. Other species identified at species level were the planktonic species
314 *Cyclotella stelligera* Cleve & Grunow, and the benthic species *Cocconeis pediculus* Ehrenberg
315 and *Nitschia amphibia* Grunow. Exluding *Alveolophora* sp., the other identified species are still
316 common today in freshwater environments and favour alkaline waters. For example,
317 *Aulacoseira granulata* is a freshwater, meroplanktonic species which prefers alkaline, eutrophic
318 waters. The species is found also in Miocene deposits and remains common today.
319
320 [Table 3]
321 [Figure 7]
322
323 The *Alveolophora* genus is currently understood to be entirely extinct as it existed only from the

Late Eocene until the end of the Miocene (Kozyrenko et al., 2008). One finding of *Alveolophora* species is dated to the Early Pliocene (Kozyrenko et al., 2008). *Alveolophora* is primarily reported from fossil localities in Asia, including the Russian Far East (Khursevich, 1994; Kozyrenko et al., 2008) and Lake Baikal (Khursevich and Fedenya, 2006). Recently, three new species of this extinct diatom genus have been described from Miocene sediments in western North America (Usoltseva et al., 2013). Previous studies indicate that all found species of *Alveolophora* are freshwater ones and that the distributions of the species belonging to this genus are regional rather than global. The *Alveolophora* sp. found in our sediment sample could not be identified to species level suggesting that it is a new, previously unknown species of this extinct genus.

DISCUSSION

Chronological constraints

The most common diatom species *Alveolophora* sp. of the sediment existed from the late Eocene to the late Miocene, between ca. 32 and 5 Ma. As the genus became extinct at the end of the Miocene, this limits the minimum age of the bone at about 5 Ma. The pollen and spore content appears to rule out the pre-Miocene, as fossil spores bearing similarities to *Pteris* are only documented in the European fossil record starting in the Miocene (Shatilova and Stuchlik, 1996). However, this inference is uncertain as few Palaeogene and Neogene deposits survive in northernmost Europe, and thus the data on the regional vegetation is scarce.

However, a more robust estimate of the maximum age can be done based on the expansion of proboscids from Africa. Proboscideans only arrived in Europe in the Early Miocene, ca. 19–17 Ma ago (Göhlich, 1999). The genus *Deinotherium* arrived in Europe in the Middle Miocene, somewhere between 16 and 13 Ma, and became extinct in the Pliocene, somewhere between 5

and 2 Ma (Göhlich, 1999; see also the NOW database: Fortelius, 2015). The probable affinity of the Suomusjärvi specimen with this genus, together with the information from the diatoms and pollen, would place the age of the find within this time frame, probably in the Late Miocene (ca. 11–5 Ma). However, the comparably small size of the specimen for the genus *Deinotherium* could even point at a late Middle Miocene (ca. 16–11 Ma) age, because the size is close to the late Middle Miocene specimens of *Deinotherium* from Austria and Germany, and there was a progressive size increase in European *Deinotherium* through time (see Aiglstorfer et al., 2014). This is, however, highly speculative, especially because the age or growth stage of the individual animal cannot be reliably estimated. Furthermore, the nutritional and general health status of the individual cannot be assessed.

In summary, a Quaternary age can be conclusively rejected based on the presence of numerous unequivocally pre-Quaternary pollen, spore and diatom types. Further constraints are provided by the presence of the diatom *Alveolophora* sp. which suggests a *minimum age* of 5 Ma, while a *maximum age* of 19 Ma is derived from the earliest appearance of proboscideans outside Africa. There is nothing in the pollen, spores, or diatoms to contradict this age bracket of 19–5 Ma.

Palaeobiogeographic significance of the Suomusjärvi proboscidean specimen

The proboscidean humerus specimen from Suomusjärvi, Finland, latitude 60˚22´N, is the northernmost Miocene proboscidean fossil found anywhere in the world so far. Even accounting for all the possible transport directions of the specimen, it could not have been drifted from very much further south, and indeed it is more likely to originate from even further north than where it was found (see the discussion below). In Eurasia, the previously northernmost proboscidean finds come from localities up to ca. 52˚N (e.g. Ermak and Bestobe, Kazakhstan, and Rothenstein, Germany), and the northernmost finds of *Deinotherium* from Germany (49–50˚N), e.g from N-Ebing Inn, Wissberg and Gau-Weinheim (NOW database: Fortelius, 2015). In North

America the northernmost finds of the Miocene proboscideans *Zygolophodon* and *Gomphotherium* come from Wood Mountain, Saskatchewan, Canada, 49˚37´N (Madden and Storer, 1985). The ca. 50˚N northern limit in the distribution of Miocene proboscidean finds has most likely been a bias caused by a lack of mammal bearing fossil localities further north, and there is no ecological or climatic reason to expect that proboscideans could not have occurred further north. In fact, the Miocene palaeobotanic records from Denmark and Iceland show a mixture of temperate and subtropical vegetation indicating subtropical climate in Northern Europe, substantially warmer than at present (Larsson et al., 2006; Grímsson et al., 2007), which is supported by the pollen and diatoms associated with the Suomusjärvi specimen (see discussion below). Humid, heavily wooded conditions prevailed throughout the Late Miocene in the proboscidean localities from Germany (Franzen et al., 2003; Costeur et al., 2013), although the habitats of *Deinotherium* further north could have been different. Most likely representing the genus *Deinotherium*, the Suomusjärvi proboscidean would have been a large woodland browser feeding primarily on leaves from trees (see e.g. Calandra et al., 2008). This would fit well with the suggested environmental interpretations.

Interpretation based on the microfossil content and environmental reconstruction

A remarkable feature of the palynoflora is that 54 % of the count consists of spores of just three types (*Pteridacidities variabilis*, *Echinatisporis* sp., and *Dryopteris*-type), presumably representing pteridophyte species of *Pteris*, *Selaginella*, and the various pteridophyte taxa producing monolete spores commonly lumped together as the *Dryopteris*-type (e.g. Moore et al., 1991). In the Neogene, all three genera (*Pteris*, *Selaginella*, *Dryopteris*) are regarded to have occurred as components in the shoreline vegetation of lakes or streams (Shatilova and Stuchlik, 1996; Grímsson et al., 2011). As these spores occur at anomalous frequencies compared with other European Miocene deposits (Fig. 8), in which pteridophyte spores occur only at very low numbers (e.g. Jiménez-Moreno et al., 2005; Larsson et al., 2006; Grímsson et al., 2011), and as

just a few spore types dominate the palynoflora, the likeliest explanation is that the bone was first deposited very close to the shore of a lake or a stream. This caused the observed over-representation of the shoreline pteridophytes which happened to occur at the site of deposition, while comparatively few pollen from the regional terrestrial vegetation are seen.

[Figure 8]

Although all the pollen and spore types found do occur in the European Miocene, we consider it probable that some Quaternary admixture has taken place during the later transport of the bone. Admixture of Quaternary pollen is suggested especially by the relatively large proportions of Chenopodiaceae and *Artemisia* (Table 1). These taxa are key components in the tundra–steppe vegetation of the cold stages of the Quaternary, while in the European Miocene palynoflora, although present, they do not typically occur at such percentages (e.g. Stuchlik and Shatilova, 1987; Jiménez-Moreno et al., 2005; Larsson et al., 2006). We note that while the unequivocally pre-Quaternary spore and pollen types were generally in good condition (see examples in Fig. 6), the pollen and spore types consistent with a Quaternary age were often much worse preserved, being superficially similar to the reworked pollen commonly seen in Quaternary glacial sediments of Fennoscandia. The observed palynoflora might best be explained as a Neogene local shoreline assemblage (with some Cupressaceae from the surrounding terrestrial vegetation included) later mixed with a smaller fraction of reworked late-Quaternary pollen (*Alnus*, *Betula*, *Juniperus*, *Pinus*, *Artemisia*, Chenopodiaceae, Poaceae, *Equisetum*) during the transport of the bone.

Pteris cretica today has a wide distribution in subtropical and tropical climates, including the Mediterranean and Black Sea regions, Madagascar, South and East Asia, Central America and the Caribbean, and Florida (Shatilova and Stuchlik, 1996). The presence of its probable close ancestor *Pteridacidites variabilis* thus suggests at least a subtropical climate at the time of bone

deposition. We note that other *Pteris* species also have a mainly subtropical and tropical distributions (Shatilova and Stuchlik, 1996), while the *Pteris* species constituting the *Pteris cretica* complex in North America occur in the tropics (Martínez and Morbelli, 2009), and thus the inference of at least subtropical conditions is likely robust to the species-level identification of our *Pteris*-type spores. Results on Miocene vegetation in Austria (Grímsson and Zetter, 2011; Grímsson et al., 2011), Germany (Uhl et al., 2006), Denmark (Larsson et al., 2006), and Iceland (Grímsson et al., 2007), showing a mixture of temperate and subtropical vegetation elements and a generally subtropical climate, preclude full-tropical conditions in northern Europe, and thus the final climatic inference becomes subtropical.

Diatoms indicate freshwater, alkaline and eutrophic sedimentation environment, i.e. the bone was stratified in a river or small lake of relatively high nutrient content. This sedimentation environment might indicate a relatively warm climate. Thus the diatom results are consistent with the pollen-based inference both in terms of depositional environment and climate.

Miocene proboscidean assemblages from Europe are typically associated with sediments indicating riparian environments or the presence of substantial waterbodies. This probably indicates a preference of these animals to seek waterbodies in order to get a regular access to drinking water and to wallow in water, similarly to modern elephants. Major Early and Middle Miocene proboscidean localities, such as German Molasse Basin localities and Sansan from France, indicate the presence of riparian, lacustrine and wetland environments (Calandra et al., 2010; Costeur et al., 2012). The early Late Miocene (Vallesian) locality of Eppelsheim in Germany, the type locality of the abundant and wide-spread European Late Miocene deinothere species *Deinotherium giganteum*, consists of fluvial deposits of the Dinotheriensande Formation deposited by the ancient Rhine River (Franzen et al., 2003). The same locality has yielded remains of the gomphotheriid proboscidean *Tetralophodon longirostris*. Pollen records from Eppelsheim indicate a floodplain environment surrounded by subtropical forests (Franzen et al.,

2003; Kaiser, 2004). The later Late Miocene (Turolian) locality of Dorn-Dürkheim 1 from Germany has provided fossils of *Deinotherium* and gomphotheres (Franzen et al., 2013). The environment of Dorn-Dürkheim 1 was suggested by Costeur et al. (2013) to have comprised both forest and patches of open vegetation based on the diverse mammal community. Moreover, e.g. the abundant and diverse record of fossil beavers suggests the presence of substantial waterbodies and river channels in the palaeoenvironment of Dorn-Dürkheim 1 (Costeur et al., 2013). The inferred riparian environment of the Suomusjärvi proboscidean are consistent with these observations.

Constraints on transport direction

The discovery of an apparently Miocene-age bone from the southern Finland presents a considerable conundrum, as no Miocene bones are known from the Nordic countries. To date, the northernmost findings are from ca. 50˚N (Fig. 8). As even deposits of Miocene age are not known from either southern Finland or the near vicinity (Rasmussen et al., 2008), the implication is that the bone must have been transported over considerable distance to the site of discovery.

One possibility for bone origin is glacial transport from the North, during one or more of the latest Quaternary glaciations. The site of discovery lies south of the Fennoscandian ice divide, and in the general direction of glacial erratic drift from the ice divide (e.g. Donner, 1989). As noted, sparse terrestrial Miocene sediments have been discovered in the northern Finland ice-divide region (Hirvas and Tynni, 1976; Tynni, 1982), presenting a possible source region. However, as the bone was found in clay representing an early-Holocene stage of the Baltic Sea (Yoldia Sea), the final transport and deposition must have been through iceberg rafting. Given the prevailing currents in the Baltic Sea, this transport phase likely had a westward direction. However, considering the great distance to closest known Miocene deposits (Fig. 8), this early-

Holocene iceberg rafting was likely preceded by other transport phases, including one or more phases of glacial and/or glacio-fluvial transport during the late Quaternary. Considering the likelihood of multiple phases and modes of transport, but with the exact number of transport phases and modes unknown, we are unable to estimate the likely region of origin with any confidence.

We note, however, that both the alkaline composition of the bone-cavity sediment and the diatom flora suggest an origin in a region of alkaline bedrock. This points towards an origin in the east, in the Russian Plain region, instead of the acidic bedrock region of the Fennoscandian Shield. The maximum transport distance is set by the maximum extent of Quaternary glaciations in northern Europe (e.g. Svendsen et al., 2004), as all credible transport mechanisms require the presence of an ice sheet. Together, these considerations suggest a possible origin in the northern part of European Russia.

The pollen, spores and diatoms found within the bone include some environmental indicators, but we are unable to better pinpoint the origin of the bone with these, especially as only sparse Miocene sediments survive in northern Europe to serve as points of comparison and Miocene environments and species compositions in northern Europe are thus poorly resolved. As noted, the presence of *Pteridacidites variabilis* suggests a subtropical climate during bone deposition. Climate reconstructions from other European sites suggest humid-subtropical-type climates (~ Köppen classification Cfa) to have prevailed widely in central and northern Europe, from Austria to Iceland (Uhl et al., 2006; Grímsson et al., 2007, 2011; Grímsson and Zetter, 2011) during the Miocene, with further indications of subtropical trees such as palms and *Engelhardia* also thriving in Denmark (Larson et al., 2006). Taken together, these evidence suggests a weak latitudinal temperature gradient in Europe. Thus, while the pollen and spore content in the Suomusjärvi bone are consistent with these palaeoclimatic reconstructions from other central and northern European sites, the bone cannot confidently be said to originate from any specific

region.

The diatoms within the bone's marrow cavity do not support transport from northern Finland as this kind of diatom assemblage has not been previously discovered from Finland. Of course, this can be due to the very sparse Miocene deposits found in Finland and thus the transport from the north cannot be ruled out. Sediment properties and the presence of *Alveolophora* sp. might suggest transport from the east (Russia) as there this species is rather common in the Miocene sediments, although most of the findings originate as far away as the Russian Far East. However, the lack of *Alveolophora* findings from the W–NW European Russia can be due to the regionally restricted occurrence of the species of this diatom genus and/or the several glaciations which have eroded the area.

CONCLUSIONS

We return here to the four questions presented in the Introduction:

1. The specimen from Suomusjärvi was identified as a partial diaphysis of the left humerus of a large proboscidean. Based on a few key morphological features and size of the specimen, it most likely represents the genus *Deinotherium*, and it is described here as cf. *Deinotherium* sp. Coming from the latitude of ca. 60˚N, and possibly originating from even further north, this is the northernmost Miocene proboscidean fossil found anywhere in the world. The previously northernmost finds, including those of European *Deinotherium*, come from localities ca. 50˚N.
2. A minimum age of 5 Ma for the bone is set based on the presence of an unidentified diatom species belonging to the genus *Alveolophora*, while a maximum age of 19 Ma is set by the earliest arrival of proboscideans to Europe. Together, these evidence confirm a Miocene age for the specimen. If the identification of the bone as *Deinotherium* sp. is

correct, the maximum age is further reduced to 13.5 Ma based on the first appearance of this genus in Europe.

3. The pollen and diatom assemblages suggest that the bone was deposited close to the shore of a lake or a stream. The pollen assemblage suggests at least a subtropical climate, which is consistent with the inferences of a subtropical climate from other Miocene sites in central and northern Europe.
4. The geographical origin (i.e. transport direction) of the bone remains poorly resolved. The discovery of the bone in early-Holocene Palaeo-Baltic clay suggests iceberg rafting as the final transport mode, however this was likely preceded by one or more phases of glacial and/or glacio-fluvial transport. The alkaline composition of the bone-cavity sediment and the generally alkaline diatom flora suggest a possible origin in the east, in the Russian Plain. However, the microfossils found cannot conclusively ascertain the region of origin as few Miocene deposits survive for comparison in northern Europe.

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use the photo of Elephas recki humerus in Fig. 3.

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Table 1. Measurements of the Suomusjärvi specimen and some European deinothere humerus specimens. Min. diaph. width = smallest latero-medial diameter of diaphysis. Min. diaph. depth = smallest cranio-caudal diameter of diaphysis. Min. diaph. circ. = smallest circumference of diaphysis.

Measurement (mm)	cf. *Deinotherium* sp., Suomusjärvi	*Deinotherium giganteum*, Munich (Stromer, 1938)	*Deinotherium giganteum*, Kettlasbrunn (measurements by J. Saarinen)	*Deinotherium thraceiensis*, Ezerovo (Kovachev and Nikolov, 2006)	*Prodeinotherium bavaricum*, Franzenbad (Huttunen, 2004, J. Saarinen)	*Prodeinotherium bavaricum*, Unterzolling (Huttunen and Göhlich, 2002)
Min. diaph. width	114	115	170	190 sin., 195 dext.	104	132
Min. diaph. depth	99	-	154	-	95	-
Min. diaph. circ.	359	-	545	-	350	420

Table 2. Pollen analysis results.

Type	Count	% of total
Pteridacidites variabilis	26	26.5
Echinatisporis sp.	15	15.3
Dryopteris-type	12	12.2
Pinus	12	12.2
Poaceae	10	10.2
Betula	6	6.1
Indet. trilete spores	6	6.1
Artemisia	3	3.1
Chenopodiaceae	3	3.1
Indet. Cupressaceae (Neogene non-*Juniperus* types)	2	2.0
Alnus	1	1.0
Equisetum	1	1.0
Juniperus	1	1.0
Total count	98	100.0

Table 3. Diatom analysis results.

Diatom species	Count	% of total
Alveolophora sp	65.5	54.6
Aulacoseira granulata	42.5	35.4
Cocconeis pediculus	3	2.5
Cyclotella stelligera	2	1.7
*Gomphonem*a sp.	2	1.7
Nitzschia amphibia	2	1.7
Nitzschia sp1	2	1.7
Nitzschia sp2	1	0.8
Total count	**120**	**100**

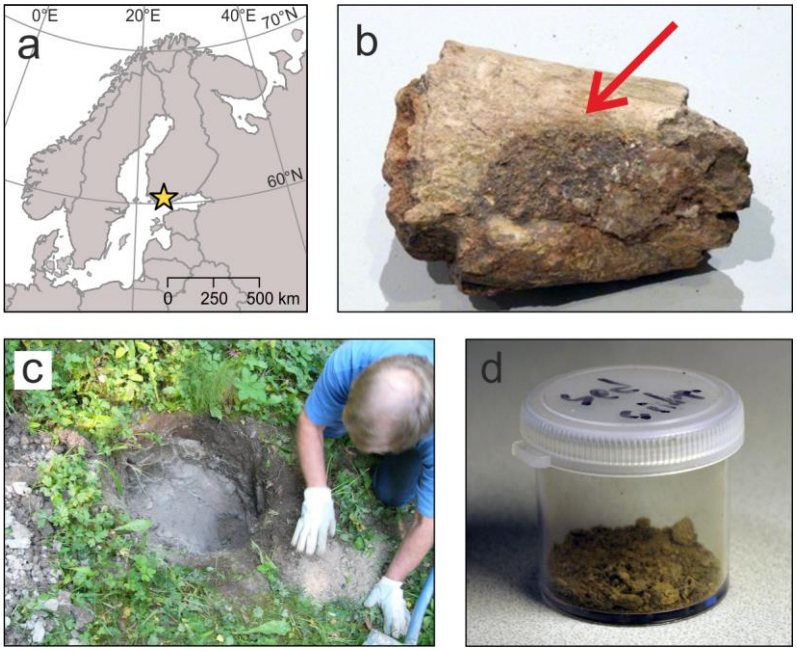


Figure 1. (**a**) Site of bone discovery. (**b**) Photograph of the bone (the brownish sediment indicated with a red arrow) (Photo: Laura Hiisivuori, the Finnish Museum of Natural History). (**c**) An excavation in 2006 at the site of discovery, showing the Yoldia Sea clay layer (light grey) in which the bone was found (Photo: Veikko Sorsa, University of Helsinki). (**d**) Some of the sediment sample on which the diatom and pollen analyses were performed.

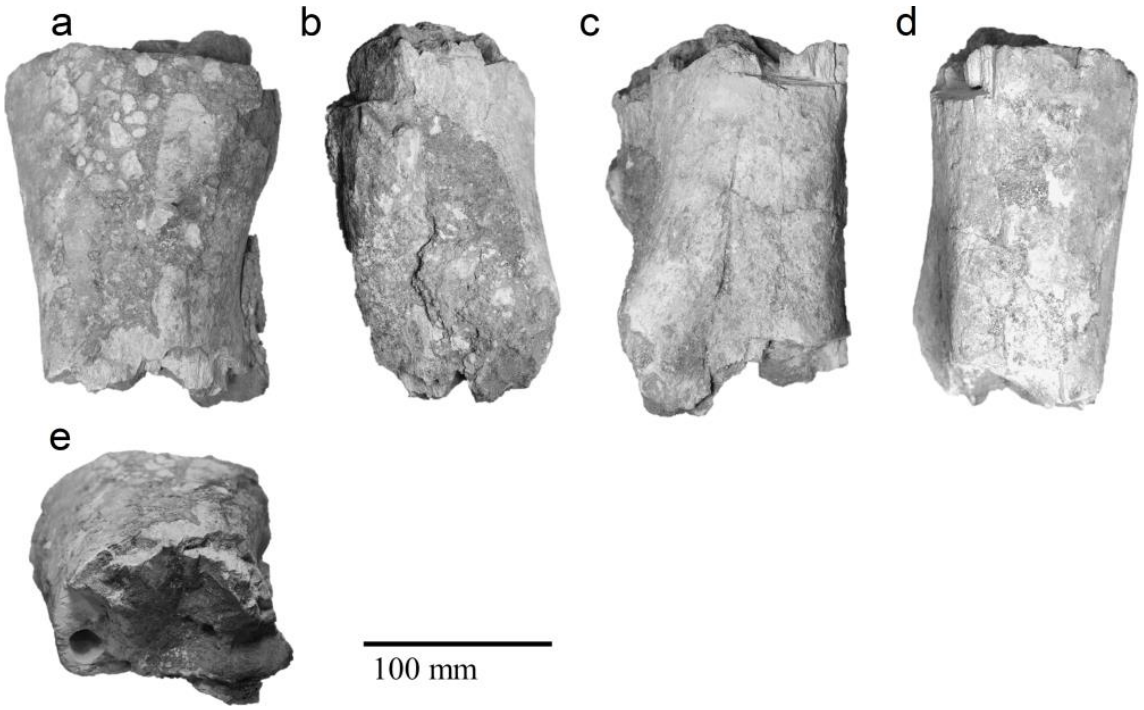
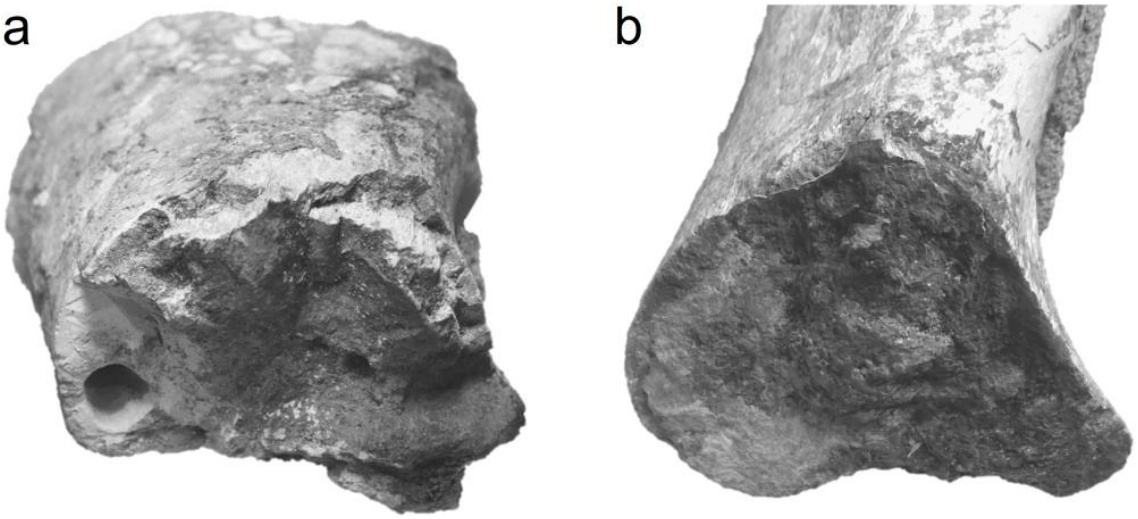


Figure 2. The Suomusjärvi proboscidean fossil (left humerus diaphysis) in (**a**) cranial, (**b**) left lateral, (**c**) caudal, (**d**) right lateral and (**e**) craniodistal view.



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918 **Figure 3.** Visual comparison of the cross-sections of (**a**) the Suomusjärvi specimen and (**b**) a
919 fossil elephant (*Elephas recki*) humerus (NHM M 14691) from Olduvai, Tanzania. Note the
920 lack of prominent crista humeri in the Suomusjärvi humerus resulting in a rounded rather than
921 triangular cross-section at the mid-shaft of the bone. The elephantid humerus figure has been
922 reversed for comparison. The photos are not in the same scale. The *E. recki* specimen from
923 Olduvai is stored at the Natural History Museum of London.

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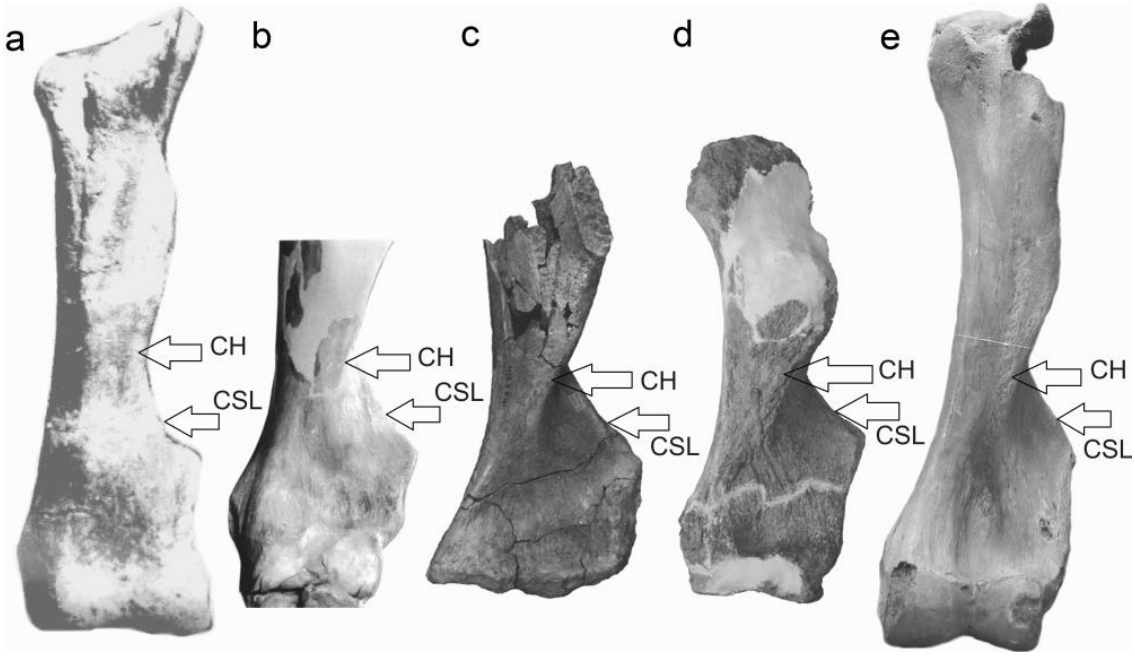
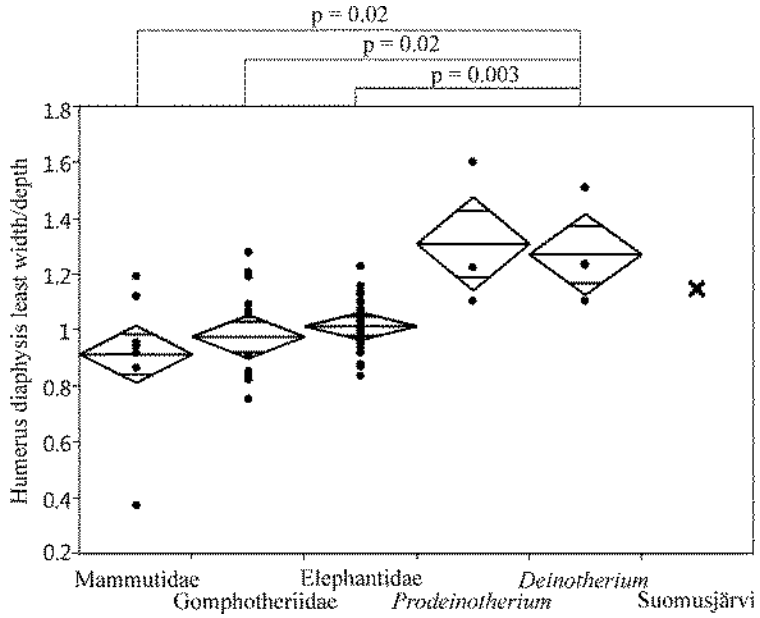


Figure 4. Examples of the humeri of *Deinotherium* (**a**), *Prodeinotherium* (**b**), *Gomphotherium* (**c**), *Mammut* (**d**) and *Mammuthus* (**e**), with arrows pointing at the crista humeri (CH) and the crista supracondylaris lateralis (CSL). Photos **c**, **d** and **e** are reversed in order to show the features as they appear in the Suomusjärvi specimen. The photos are not to the same scale. Note the strongly reduced and inconspicuous crista humeri of *Deinotherium* compared to the other taxa. **a**. *Deinotherium thraceiensis* (Deinotheriidae) from Ezerovo, Bulgaria (Kovachev and Nikolov, 2006), **b**. *Prodeinotherium bavaricum* (Deinotheriidae) from Franzensbad, Czech Republic (Huttunen, 2004), **c**. *Gomphotherium subtapiroideum* (Gomphotheriidae) from Sandelzhausen, Germany (Göhlich, 2010), **d**. *Mammut americanum* (Mammutidae) from Hidalgo, Mexico (Bravo-Cuevas et al., 2015) and **e**. *Mammuthus primigenius* (Elephantidae) (SMNS 6316.2.6.82.2) from Lampertheim, Germany (J. Saarinen, specimen stored in Staatliches Museum für Naturkunde, Stuttgart). Photos are reproduced with permissions from the journals (**a**, **b**, **d**) or publishers (**c**).



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955 **Figure 5.** Minimum width / minimum depth of the narrowest part of humerus diaphysis for
956 proboscidean groups. Mean values are indicated by mean diamonds in which the middle line
957 shows the mean and the upper and lower lines represent 95% confidence limits. The deinotheres
958 have on average larger width in relation to depth than the other families (significant differences
959 in mean width/depth between *Deinotherium* and Elephantidae, Gomphotheriidae and
960 Mammutidae are indicated as p-values in the figure), and the Suomusjärvi specimen fits closer
961 to the average of deinotheres than to the average of the other proboscideans in this respect. The
962 data for this comparison is gathered from literature (Göhlich, 1998, 2010; Huttunen and
963 Göhlich, 2002; Christiansen, 2004; Kovachev and Nikolov, 2006; Ferretti, 2010, Tsoukala and
964 Mol, 2014; Bravo-Cuevas et al., 2015) and from specimens measured by J. Saarinen.

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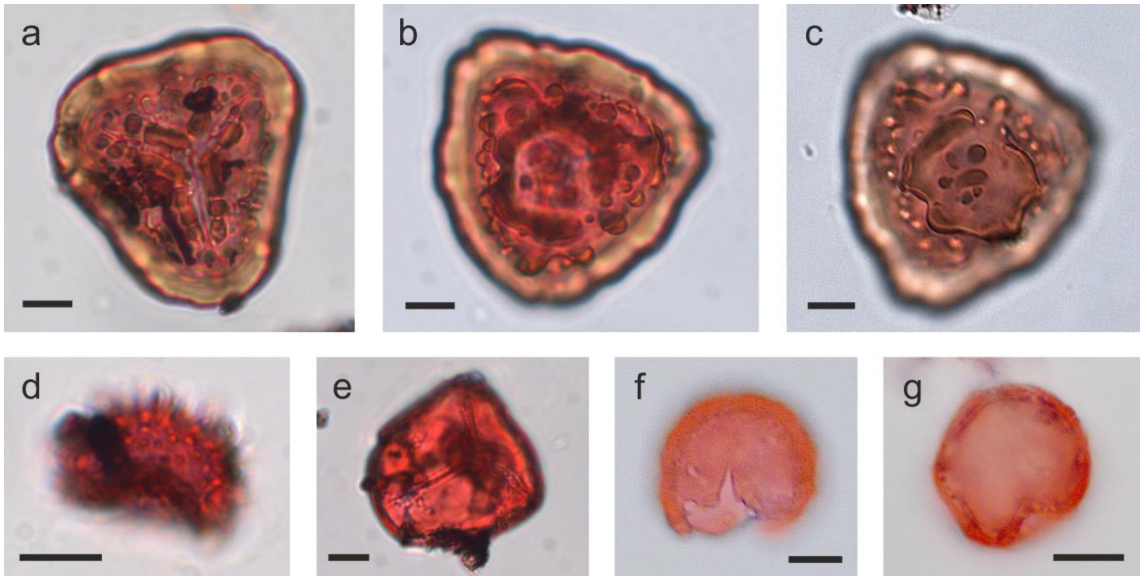

Figure 6. Micrographs of Miocene palynomorphs found in the Suomusjärvi bone: (**a**) *Pteridacidites variabilis*, specimen 1, proximal view, 400× magnification; (**b**) *Pteridacidites variabilis*, specimen 2, distal view, 400×; (**c**) *Pteridacidites variabilis*, specimen 3, distal view on surface ornamentation, 400×; (**d**) *Echinatisporis* sp., 600×; (**e**) indet. trilete spore, 400×; (**f**) indet. Cupressaceae, specimen 1, 400×; (**g**) indet. Cupressaceae, specimen 2, 1000× in oil immersion. Scale bars = 10 μm.

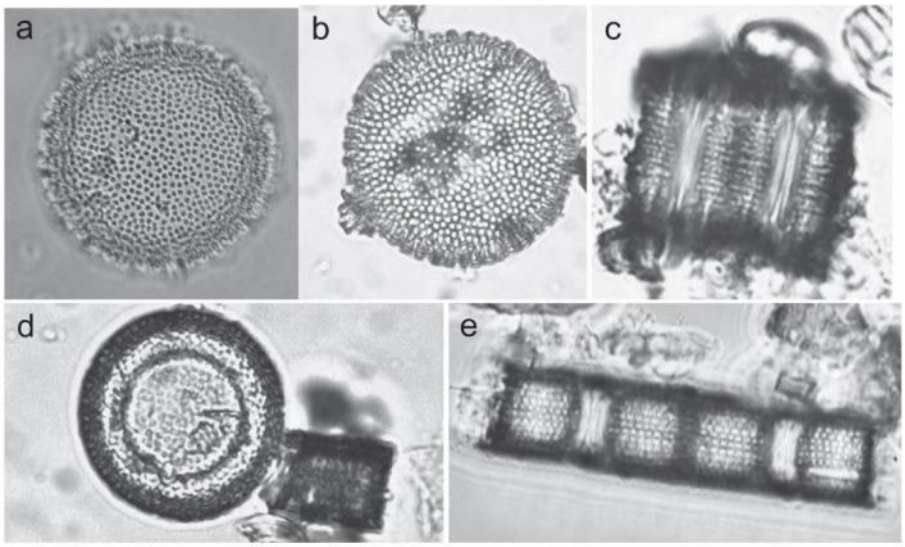

Figure 7. The most common diatom species in the sample: (**a, b, d**) *Alveolophora* sp. (valve view); (**c**) *Alveolophora* sp. (mantle view); (**e**) *Aulacoseira granulata* (mantle view).

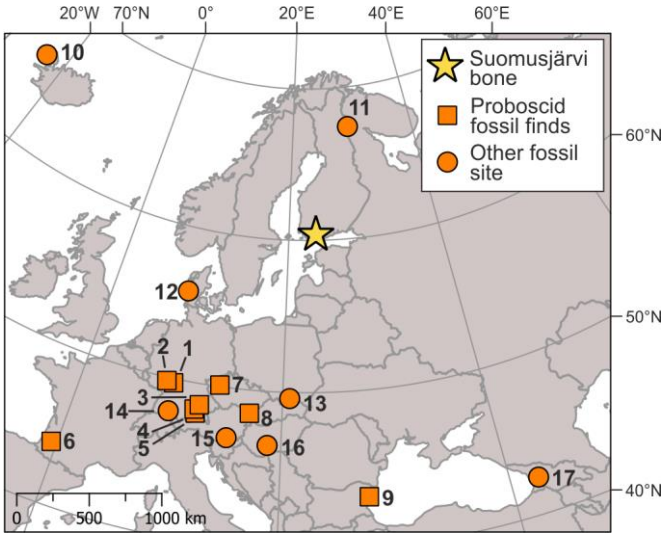

Figure 8. Map showing the site of bone discovery and locations of Neogene/Miocene proboscid and other fossil sites referenced in the text. Names and references for the numbered sites: **1**, Eppelsheim (Fortelius, 2015); **2**, Dorn-Dürkheim 1 (Fortelius, 2015); **3**, Sandelzhausen (Fortelius, 2015); **4**, Unterzolling (Fortelius, 2015); **5**, Munich (Fortelius, 2015); **6**, Sansan (Fortelius, 2015); **7**, Franzensbad (Fortelius, 2015); **8**, Kettlasbrunn (Fortelius, 2015); **9**, Ezerovo (Fortelius, 2015); **10**, Iceland (Grímsson et al., 2007); **11**, Naruskajärvi (Hirvas and Tynni, 1976; Tynni, 1982); **12**, Sønder Vium (Larsson et al., 2006); **13**, Nowy Sącz and Nowy Targ-Orawa Basins (Stuchlik and Shatilova, 1987); **14**, Bohlinger Schlucht (Uhl et al., 2006); **15**, Lavanttal Basin (Grímsson and Zetter, 2011; Grímsson et al., 2011); **16**, Pannonian Basin (Jiménez-Moreno et al., 2005); **17**, Western Georgia (Stuchlik and Shatilova, 1987; Shatilova and Stuchlik, 1996).